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CONCERNING HEAT DEFOLIATION

[Following is a translation of an article by Julius Wiesner in the German-language periodical Berichte der Deutschen Botanischen Gesellschaft (Reports of the German Botanical Society), Vol 22, 1904, pages 501-505.]

1. In continuation of my notes on "summer defoliation" and "budding defoliation" published earlier in these Reports (Vol 22, 1904, pages 64-72 and pages 316-323), I present here some observations on the "heat defoliation" which sets in during extreme summer heat and simultaneous great dryness of the ground, and which I only referred to incidentally in the two articles mentioned.

The enormous heat of the past summer (1904) gave ample opportunity for observations of heat defoliation, and in the months of June and July 1904, both in Baden (Lower Austria) and in Vienna and vicinity, I made many relevant observations. The beginning of August I went to North America, principally in order to do studies in the Yellowstone area concerning the utilization of light and in connection with that also concerning the light climate. I also intended to make observations there on heat defoliation, and hoped for rich harvests under the impression that extraordinary heat would prevail there, too, this summer. The extraordinary heat of the sun was held to be a phenomenon prevailing all over the earth, and many connected it with the eleven-year sunspot cycle. But in all the states of North America that I visited between New York and Wyoming, I heard it universally agreed that this particular summer was distinguished by particular coolness, and I found that confirmed on the whole by the meteorological reports that I was able to see afterwards. My crop of observations on heat defoliation in North America was therefore not so big as I had expected. Nevertheless I was able to make several very interesting observations there on this phenomenon.

2. As in all forms of defoliation, we encounter in heat

defoliation an extraordinary diversity of individual forms, but both the causation of the phenomenon and its course seem more varied than one might suppose from superficial consideration.

It is the rule that only the foliage struck directly by the sun "burns up," as it is often expressed, that is is killed by the heat and immediately falls. But on lindens and elms I have often made the observation that the reflected radiation from walls and cliffsides led like direct radiation and in quite a destructive way to heat defoliation.

It is also the rule that, as I shall explain more fully later, while it is foliage directly struck by the sunlight that "burns up," it is commonly not that part which is peripherally located, but that situated at a greater or lesser depth in the treetop. But in the case of foliage leaves whose tracheal system is not developed or is incompletely developed and which as a result of intense transpiration of the fully developed foliage is subjected to "descending streams of water," it is precisely the most peripherally situated foliage that "burns up" from the heat earliest, etc.

3. I have found it confirmed over and over again that heat defoliation occurs only when the ground on which the plants under observation stand has been dried out, or at any rate has not been supplying the plant with the requisite amount of water. Where trees or bushes were standing on abundantly watered meadows, no heat defoliation occurred in spite of great and long-lasting radiation. It seems that with a sufficient supply of water the foliage leaf can endure the most intense radiations of the hot period without being damaged, and there should be no doubt that heat defoliation, i.e. the killing of the leaf in consequence of the heat and the consequent shedding of foliage, is due to excessive transpiration; i.e. the evaporation conditioned by intense radiation is no longer adequately compensated for by water from the ground.

4. The commonest form of heat defoliation is characterized by the fact that as a rule it is not the foliage situated on the extreme periphery of the treetop, and thus most abundant struck by the sun's rays, but the foliage lying deeper in the treetop, which however must always be struck by the direct (parallel) sunlight, which "burns up" and falls off.

This relationship seems at first glance paradoxical, but riper reflection leads to the realization that this very relationship holds the key to the explanation of "heat defoliation."

As I found in my studies of the "photic ration" of the

plants, in the treetop the intensity of the total light decreases continuously from the periphery to the center; but according to those studies it is only diffuse light that suffers that attenuation, and not the sunlight in the narrower sense, namely the parallel radiation, which works with equal intensity whether it strikes the foliage leaf in the periphery or deep inside the treetop. But as the foliage is subject to a greater heat radiation the greater the open area of sky that it faces, it is easy to see that leaves inside the treetop which are struck by the sun are exposed to a greater heating than those situated on the circumference of the treetop. This intense heating of the leaves situated on the inside of the treetop but radiated by the sun is the principal cause and the usual cause of heat defoliation. Exceptional cases have already been mentioned, and it should also be noted that many species of trees have such heat-sensitive foliage that even the peripherally situated leaves "burn up."

5. Unquestionably numerous woody plants, both deciduous ones and conifers, are subject to heat defoliation, but whether all are remains an open question. It is a fact that the inclination to it is more marked in some species than in others, and that each leaf in the course of its development also withstands the effects of heat in differing degree.

As concerns the first point, I should designate the horse chestnuts, lindens, elms, and locusts as the trees that are subject to heat defoliation in especially noticeable degree. Carpinus, Fagus, Colutea arborescens, and Evonymus europaeus and verrucosa are more resistant. The laurel is very little subject to heat defoliation. In Ligustrum vulgare I have observed no heat defoliation (Baden and Vienna) in spite of close observation, even in the sunniest places.

As to the developmental state of the leaf, in general the oldest leaves fall victim to heat defoliation first. This is true of the leaves of both broad-leaved and needle-bearing plants. Young fir needles (Pinus) are far more resistant than old ones. Quite young foliage, in which the tracheal system is undeveloped or incompletely developed, may be killed by the heat early for special reasons, as has already been mentioned.

6. Many woody plants have the capacity to protect themselves from heat and prevent heat defoliation. As examples of this I mention Cornus mas and Cornus sanguinea, and also Viburnum lantana. Under conditions of intense radiation of the foliage and great dryness of the ground the leaves of the plants named immediately hang down limply, so that they are protected against the effect of the most intense sunlight, namely from the effect of the sun at its highest elevation.

It is easy to see that the leaf hanging down vertically can be struck by the rays of the sun at its height only at very small angles, so that at the very time of most intense radiation it will be radiated only to a very slight degree.

7. The mode of separation of the foliage appears to be no other than that found in the other forms of defoliation. In all the broad-leaved trees examined by me the leaf base of the "burned up" foliage was succulent at the time of onset of heat defoliation, and within this moist part of the leaf base the same anatomical changes occurred in the tissue as prepare the way for the separation of the leaves in the autumnal defoliation.

Heat defoliation is due to the effect of the parallel (usually direct, more rarely reflected) rays of the sun, and manifests itself first in a destruction of the chlorophyll.

Separation of the leaf which is dying as a result of the heat is an organic process, as in all defoliation.

8. In general I did not encounter the phenomenon of heat defoliation in America in those pronounced forms in which I had seen it shortly before in the above-mentioned districts of Europe. In New York I saw in the parks (Central Park, Union Square, Madison Square, etc.) elms, lindens, maples, and hornbeams (*Carpinus*) standing at the side of the street more or less affected by heat defoliation, while trees of the same species standing in well-watered grass-grown areas showed the phenomenon of summer defoliation, but not heat defoliation. In the general vicinity of Niagara Falls I could follow step by step the phenomenon of summer defoliation, but observed not a single pronounced case of heat defoliation. In St. Paul and Minneapolis, too, I observed almost no heat defoliation; only scattered specimens of *Acer negundo* in dry locations gave evidence of more or less pronounced heat defoliation.

In the splendid big park beyond the dense housing complex of Chicago (Washington and Jackson Park), where the trees stand on abundantly watered lawns, there was not so much heat defoliation to be seen as in the much less well-kept gardens in downtown Chicago (Garfield Park, etc.), where elms, lindens, and maples presented very striking forms of heat defoliation.

In the environs of Chicago the extremes were taken by elms (*Ulmus americana*) and poplars (*Populus carolinensis*); the former had suffered badly under the heat almost everywhere, while the latter showed summer defoliation, but no trace of heat defoliation. The picture changed remarkably with altitude above sealevel; at Billings (950 m) and still more in

Livingston (1367 m) and Mammoth Hot Springs (Yellowstone National Park, 1946 m) the poplars (forms of Populus carolinensis, P. tremuloides, and our P. alba, which occurs in North America, according to my observation, often in small-leaved form) showed definite and often very pronounced heat defoliation.

Heat defoliation showed up particularly noticeably at great altitudes (8000 English feet and above) in Pinus murrayana, which is the predominant species of tree in the Yellowstone area. It is chiefly the older needles that fall victim to heat defoliation. I saw the same thing in Baden near Vienna in the black pine, which this summer (July) shed its needles so abundantly because of the heat that in places the ground appeared to be covered with "burned up" needles.

It was very noticeable that in Pinus murrayana it was the shoots situated inside the treetop but still shone upon by the sun that "burned up." They were distinguished by a bright yellow-brown color from the shoots that had remained intact. This phenomenon, though in much less marked form, was also exhibited by the black pine when attacked by heat defoliation.

The remarkable phenomenon of the occurrence or intensification of heat defoliation (in poplars and Pinus murrayana) with increase in altitude above sealevel has its cause in the photic climate. My studies of this matter, especially those undertaken in the Yellowstone area, yielded not only a numerically based confirmation of the known fact that with equal cloudiness of the sky and equal elevation of the sun the light intensity rises with the altitude, but also the previously unestablished fact that with equal cloudiness and equal elevation of the sun the intensity of the direct (parallel) radiation, in comparison to the radiation diffused in an infinite number of directions, rises with the altitude.

Now since heat defoliation depends not on the diffuse daylight, but on the parallel (usually direct, more rarely reflected) solar radiation, it is clear that for many species of trees the conditions for the onset of heat defoliation will be created only with increasing altitude above sealevel.

An intensive analysis of heat defoliation and of the biology of defoliation in general, based on experimental evidence, I reserve, as I have stated on similar previous occasions, for a later date.